

PLUMAGES OF THE REDHEAD, Aythya americana:
Upper left, male four months of age in postjuvenal molt
Upper right, male ten weeks of age
Middle left, adult female in spring
Middle right, adult male in winter and spring
Lower left, adult female in summer with day-old chicks
Lower right — Eclipse plumage of one-year-old male

## GROWTH, WEIGHTS, AND PLUMAGES OF THE REDHEAD, AYTHYA AMERICANA<sup>1</sup>

### BY MILTON W. WELLER

DESPITE the intense interest in waterfowl shown by aviculturists, ornithologists, wildfowlers, and wildlife managers, surprisingly little has been published concerning their growth, weights, and plumage development. Growth and plumage development probably have been studied little because the precocial young are difficult to examine periodically in the wild, and few investigators have reared waterfowl for growth studies. At the Delta Waterfowl Research Station, in southern Manitoba, excellent facilities are available for rearing many species of ducks. This equipment was used during the present study to investigate the growth of the young Redhead (Aythya americana). Some of the birds were held in captivity as long as five years in order to observe plumage changes in adults. In addition, data were gathered on plumages and weights of wild adults during a concurrent study of the breeding biology of the Redhead.

### ACKNOWLEDGMENTS

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Unpublished field data were provided by Alex Dzubin, Peter Hanson, and Herbert J. Miller (Michigan Federal Aid Waterfowl Research Project 45-R).

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#### MATERIALS AND METHODS

Sources of birds and hatchery techniques.—Eggs were collected from nests of wild Redheads and placed in still-air incubators at 99° F. Newly hatched ducklings were held in the incubators until dry. In 1952, the ducklings were put in small, heated pens and later in larger enclosures. In 1953, they were placed in a pen under heat lamps and the pen was enlarged as the birds

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grew. At six to seven weeks of age they were moved to an outdoor enclosure large enough to permit flying. Adults were held in a heated building in winter and spent the summer outdoors in large enclosures.

Juveniles were fed turkey pellets and hard-boiled egg until two weeks old, then large poultry pellets and natural foods, such as duckweed (*Lemna minor* and *L. trisulca*). Adults were fed poultry pellets, cereal grains, and duckweed.

Observations of wild juveniles were obtained in two ways. Ducklings were dyed in the egg in the manner described by Evans (1951) and later observed and collected. In addition, ducklings captured in banding traps of the U.S. Fish and Wildlife Service were measured and marked. Birds too small to be banded were toe-punched. Marked Redheads habitually returned to the traps for food and were re-measured when a period of at least one week had elapsed between the original marking and the recapture.

Wild juveniles and adults were obtained in various parts of Manitoba from banding traps of the U.S. Fish and Wildlife Service, the Delta Waterfowl Research Station, and Ducks Unlimited. Nesting females were weighed and examined by the author in Manitoba in 1954 and 1956 and in Utah in 1955. At first they were captured with a drop trap similar to that described by Sowls (1949) and later with an automatic trap with a drop-door released by the hen when she entered (Weller, 1957).

Birds taken by hunters in the Delta Marsh and at Lake Winnipegosis during 1952 and 1953 also were examined.

Measurements.—Sizes of the samples of birds measured are shown by sex and age in Table I. During 1952, the growth of 55 hatchery-reared Redheads was studied. Birds were weighed weekly for the first 10 weeks, and then at 12 and 16 weeks of age. During 1953, Redheads were weighed at weekly intervals until 10 weeks old.

Weights of juveniles were recorded to the nearest one-tenth gram while the birds were under three weeks of age and to the nearest gram thereafter. Birds were weighed when the plumage was dry and at approximately the same time each day to prevent the complication of the pronounced daily variations in weight noted in some species (Baldwin and Kendeigh, 1938; Blake, 1956). Weights of adults were recorded in pounds and half-ounces.

Measurements of the exposed culmen and tarsus of juveniles were made with a thin plastic or metal ruler. This method allowed speedy handling of live birds in the field and in the hatchery and yet gave measurements of suitable accuracy for growth studies. Tests with dividers indicated that accuracy to within one-half millimeter for the culmen and one millimeter for the tarsus was attained. The tarsal measurement included the tarsometatarsus and the condyles of the tibiotarsus and the digits.

Scapular and flank pterylae were measured to the nearest one-half centi-

TABLE 1
Size of Samples of Hatchery-reared Redheads Measured During 1952 and 1953

|      |        |    | Age in Weeks |    |    |    |    |    |    |    |    |    |    |
|------|--------|----|--------------|----|----|----|----|----|----|----|----|----|----|
|      |        | 1  | 2            | 3  | 4  | 5  | 6  | 7  | 8  | 9  | 10 | 12 | 16 |
| 1952 | male   | 7  | 14           | 17 | 17 | 17 | 17 | 16 | 27 | 25 | 21 | 18 | 17 |
| 1952 | female | 9  | 18           | 21 | 21 | 21 | 20 | 20 | 28 | 28 | 23 | 18 | 13 |
| 1953 | male   | 8  | 8            | 25 | 24 | 24 | 25 | 25 | 24 | 24 | 21 | _  | _  |
| 1953 | female | 15 | 14           | 33 | 32 | 30 | 32 | 31 | 32 | 31 | 30 | _  | _  |

meter from the base of the anterior feathers to the tip of the longest posterior feather of the tract. The longest or ninth primary, the middle or sixth secondary, the longest tertiary, and the center tail feathers, were chosen for measurement and their lengths were recorded in millimeters from the base to tip with curved feathers flattened.

Terminology for plumage is that used by Dwight (1900), Forbush (1925), and Witherby *et al.* (1943), and terminology for color is that advised by Palmer and Reilly (1956).

## GROWTH AND SEASONAL CHANGES IN BODY WEIGHT

Weights of newly hatched ducklings and increase in weight were reported for a few European anatids by Heinroth (1928:132–229) and Portmann (1950: 525). A more detailed study of the Tufted Duck (Aythya fuligula) was made by Veselovsky (1951), who weighed five ducklings every five days from hatching to 55 days of age. Southwick (1953) recorded weights for eight species of ducks reared in the hatchery of the Delta Waterfowl Research Station but data were not taken after six weeks of age and sexes were not differentiated. Elder (1954) presented data on growth of a small number of Redheads used as controls in his study of the oil gland.

Growth of the embryo.—Data were gathered from 23 embryos of three clutches of eggs. Preserved embryos were weighed immediately after being rolled on a blotter. A typical exponential curve characteristic of early growth in body weight (Brody, 1945: 486–492, and others) is apparent (Fig. 1).

Growth of hatchery-reared juveniles.—Three to four grams were lost during the first 24 hours as the feathers dried. Thereafter, body weight increased rapidly (Fig. 2). Males were heavier than females by the second week and remained so throughout life. The greatest increase in weight occurred during the fourth to sixth weeks.

Growth was slightly more rapid in birds reared in 1952 than in 1953,

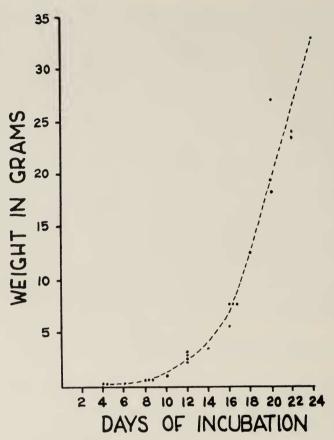


Fig. 1. Scatter diagram of the weights of 23 Redhead embryos.

especially at ages of four to seven weeks. However, during the eighth week of life, weights for the sample in 1952 decreased to the level later reached by birds of the same age in 1953. The larger pen used during the latter year may have permitted more activity and prevented the rapid addition of weight recorded in 1952. Other conditions, such as feeding and pen-cleaning, were identical. The decline in weight observed in 1952 occurred, however, during the period of most rapid growth of the remiges. While the averages for 1953 show no such decline, weights of some individuals did. These data suggest that the period of remex formation is one of great stress. Individuals vary in the amount of weight they lose but few gain during this period. Similar weight losses during fledging in passerines are well known (Edson, 1930). Peters and Müller (1951) and Mrs. Margaret Nice (in litt.) have observed such losses in gulls (Larus sp.).

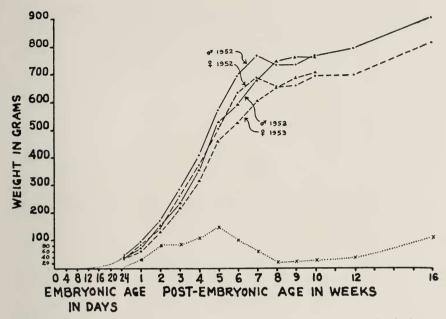


Fig. 2. Average cumulative growth in body weight in hatchery-reared Redheads (upper four curves) and average weekly increment in grams for both sexes and years (lower curve).

In order to determine the effects of handling on growth in weight, a group of 24 hatchery-reared birds was weighed during the first day of life and placed in a pen where they remained undisturbed for eight weeks. A scatter diagram of weights of 19 of these birds and 26 which were handled weekly is shown in Figure 3; there was no obvious effect of handling. A similar comparison was made by Baldwin and Kendeigh (1938); they found no statistical difference between weights of sparrows handled frequently and those trapped only once.

Growth of wild juveniles.—Although embryos in 26 nests were dyed, only six dyed broods were observed and two members of one brood collected. In general, the growth of wild juveniles was quite similar to that of those reared in the hatchery. The two dyed ducklings which were collected differed greatly in size, one (a male, 189 grams) being considerably below and the other (a female, 256 grams) slightly above the hatchery average (Table 2). Additional data were obtained from four birds dyed by Alex Dzubin near Minnedosa, Manitoba; these also are compared with hatchery averages in Table 2. Two weighed slightly more and two less than hatchery average.

Ten males and 17 females were recaptured in banding traps at least once. The increments in body size between periods of capture were compared with the data for hatchery-reared birds (1952), using the initial weight of the

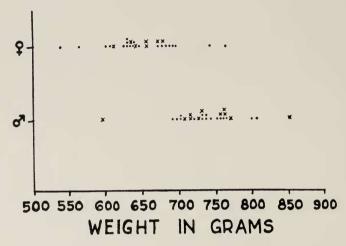


Fig. 3. Scatter diagram of weights of eight-week-old Redheads comparing birds handled each week  $(\bullet)$  to those handled only twice  $(\times)$ .

wild bird as a basepoint on the curve for hatchery birds. Wild birds tended to be similar in weight to hatchery birds from two to four weeks and heavier during the eighth and ninth weeks. Because the exact ages of the wild individuals were unknown, the relationship of body weight to culmen length in each group was also compared. Wild birds were slightly heavier than hatchery-reared birds of similar culmen length throughout life. Three of eight wild males and one of five females measured during the fledging period lost weight. Losses were similar in extent to those in hatchery birds and averaged about 50 grams for both groups.

Weights of immature and adult Redheads.—Weights of immature and adult waterfowl have been better studied than those of non-flying juveniles because of the abundance of data obtainable from hunters' bags and banding stations. Notable contributions to our knowledge of duck weights have been made by Leopold (1919, 1921); Phillips (1923–26); Bennett (1938:5–6); Kortright (1943); Bellrose and Hawkins (1947); Mann, Thompson, and Jedlicka (1947); and Nelson and Martin (1953). DuMont and Swenk (1934) and Elder (1946) analyzed the weights of the Canada Goose (Branta canadensis) and Elder (1955) presented data on weights of Pink-footed (Anser arvensis) and Greylag (A. anser) geese.

Weight data from the present study are shown in Table 2 and Figure 4. Only data from wild Redheads are presented because weights of birds housed indoors in winter in Manitoba cannot be considered comparable with those of birds wintering in the southern United States.

TABLE 2

Measurements of Six Known-age Redheads Compared to Averages for Hatchery
Redheads of Equivalent Age

|                | MAL                         | ES            |              | EMALES       |  |
|----------------|-----------------------------|---------------|--------------|--------------|--|
|                | Wild                        | Hatchery Avg. | Wild         | Hatchery Avg |  |
|                | (22-23                      | 3 days)       | (22-23 days) |              |  |
| Weight (grams) | 189                         | 277           | 256          | 251          |  |
| Culmen         | $28^{\scriptscriptstyle 1}$ | 32            | 31           | 31           |  |
| Tarsus         | 35                          | 47            | 39           | 44           |  |
| Tail           | 17                          | 21            | 23           | 19           |  |
|                | (35                         | days)         | (2           | 7 days)      |  |
| Weight         | 495                         | 546           | 409          | 325          |  |
| Culmen         | 37                          | 39            | 34           | 35           |  |
| Tarsus         | 50                          | 52            | 48           | 48           |  |
| Tail           | 37                          | 40            | 35           | 31           |  |
| Scapulars      | 80                          | 88            | 55           | 57           |  |
| Flank          | Complete                    | Complete      | 100          | 108          |  |
| Primaries      | Starting                    | 18            | _            | _            |  |
| Secondaries    | 2                           | 19            | _            | _            |  |
| Tertiaries     | 22                          | 32            | 5            | 13           |  |
|                | (47                         | days)         | (3           | 2 days)      |  |
| Weight         | 849                         | 733           | 312          | 420          |  |
| Culmen         | 46                          | 44            | 32           | 33           |  |
| Tarsus         | 54                          | 54            | 44           | 49           |  |
| Tail           | 51                          | 53            | 32           | 36           |  |
| Scapulars      | 135                         | 135           | 50           | 70           |  |
| Flank          | Complete                    | Complete      | 90           | 112          |  |
| Primaries      | 69                          | 77            | _            | _            |  |
| Secondaries    | 62                          | 65            |              | _            |  |
| Tertiaries     | 72                          | 77            | 5            | 23           |  |

<sup>1</sup>All linear measurements are expressed in millimeters.

The average weights of the various age and sex groups observed at Lake Winnipegosis in mid-September (Table 3) showed a pattern similar to that recorded for several other species of ducks by Mann, Thompson and Jedlicka (1947) and Bellrose and Hawkins (1947), and for geese by Elder (1946, 1955): adult males were heaviest, adult females and immature males were similar in weight, and immature females were lightest.

The body weight of the Redhead was greatest prior to migration, as is shown by comparing the average fall weights of Redheads in Manitoba with those in Michigan. Adult birds weighed in Michigan in October averaged seven to eight ounces lighter than Redheads weighed at Lake Winnipegosis, Manitoba, in early October (see Table 3, "post-molt"). These samples are probably from the same population, since many Redheads from Manitoba

pass through Michigan during the fall migration (Robbins, 1949; Brakhage, 1953).

Adequate samples of Redhead weights taken south of Michigan in late fall or winter are not available but presumably the weight lost in fall migra-

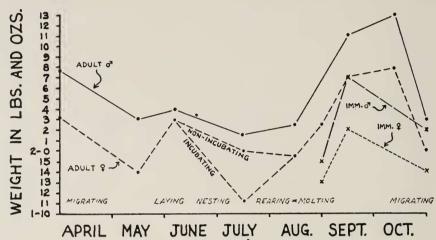


Fig. 4. Average weights of Redheads weighed on or near the breeding grounds.

TABLE 3 SAMPLE SIZE, SOURCE, AND AVERAGE WEIGHTS OF IMMATURE AND ADULT REDHEADS

| Age Area              | Source        | Stage of           | Average weight Male Female |          |     |         |
|-----------------------|---------------|--------------------|----------------------------|----------|-----|---------|
| .ge / (red            | 300100        | Annual Cycle       | No.                        | Lbs. Oz. | No. | Lbs. Oz |
| ADULT (Second         | Summer of Li  | fe)                |                            |          |     |         |
| Michigan <sup>1</sup> | Banding       | Spring Migration   | 1157                       | 2:7      | 485 | 2:3     |
| Manitoba              | Banding       | Spring Migration   | 32                         | 2:3      | 15  | 1:14    |
| Utah                  | Nest Trap     | Parasitic          | _                          |          | 40  | 2:3     |
| Utah                  | Nest Trap     | Incubating         | _                          |          | 6   | 1:11    |
| Manitoba              | Collected     | Courtship          | 7                          | 2:4      | _   |         |
| Manitoba <sup>2</sup> | Banding       | Pre-Molt           | 33                         | 2:1      | 71  | 2:0     |
| Manitoba              | Banding       | Early Molt         | 10                         | 2:2      | 41  | 1:15    |
| Manitoba              | Bagged        | Post-Molt          | 51                         | 2:11     | 19  | 2:7     |
| Michigan <sup>1</sup> | Bagged        | Fall Migration     | 40                         | 2:3      | 52  | 2:0     |
| IMMATURE (FI          | ying young of | the year)          |                            |          |     |         |
| Manitoba              | Banding       | Fall Concentration | 148                        | 1:15     | 172 | 1:13    |
| Manitoba              | Bagged        | Fall Concentration | 15                         | 2:7      | 15  | 2:2     |
| Michigan <sup>1</sup> | Bagged        | Fall Migration     | 118                        | 2:2      | 135 | 1:14    |

<sup>&</sup>lt;sup>1</sup>Data from Michigan Federal Aid Project 45-R. <sup>2</sup>Data from Peter G. Hanson.

tion is regained during winter and spring. An increase in weight is usual at this time among passerines (Wolfson, 1945). During the spring migration through Michigan (April), Redheads averaged three to four ounces heavier than birds weighed there in the fall (Table 3). Birds captured after arrival in southern Manitoba in late April and May averaged four to five ounces lighter than birds weighed in Michigan in April.

After the spring migration, females gained weight rapidly, as was shown by comparing weights of birds captured in nest traps in Utah with those captured in Manitoba in spring. This difference in weight was not due to differences in average size of Utah and Manitoba birds, for culmen measurements of the two groups were the same. Rather, it was due to intensive feeding following migration and to the growth of ovarian tissue. The ovary, oviduct, and eggs of one female collected during the laying period constituted one-eighth of the body weight, while the reproductive tract of a non-breeding female in August was only 1/2000 of its total weight. Witschi (1956:310) presented similar data for the Starling (Sturnus vulgaris). During the laying period, the weight of the female Redhead nearly equals that of the male (Fig. 4).

Redhead females laying parasitically in the nests of other birds gradually declined in weight and continued to decline during incubation (Fig. 5). (No birds were captured during normal laying.) A weight loss during the period of laying and incubating was observed in Ring-necked Pheasants (*Phasianus colchicus*) by Kabat, Thompson, and Kozlik (1950) but Richdale (1947) found that Yellow-eyed Penguins (*Megadyptes antipodes*) lost weight during laying, then regained it during incubation.

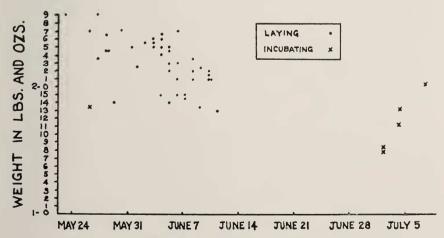


Fig. 5. Scatter diagram of the weights of laying (parasitically) and incubating females captured in Utah in 1955.

Redhead females trapped in July at Lake Winnipegosis averaged three ounces lighter than birds weighed during the laying period in Utah. Some of these birds, examined by Peter Hanson of Ducks Unlimited and myself, had brood patches; others did not and probably were non-breeders. Thus the lowest weight is reached during the period of molt, when environmental temperatures are high. Two flightless females were weighed in the Delta Marsh but their weights were not significantly different from those of other females which were molting only body feathers and which were captured at the same time of the year.

After molting, birds loaf and feed and attain their greatest weight. The heaviest bird recorded was a male taken at Lake Winnipegosis on September 20, 1952, which weighed three pounds, one and one-half ounces.

By mid-September, the average weight of immature birds found in hunters' bags at Lake Winnipegosis was five to eight ounces greater than that of immature birds at Delta during August and early September. Many of the birds shot at Lake Winnipegosis probably were early-hatched young which had flown north from their place of rearing to isolated northern lakes to loaf and feed.

## GROWTH OF THE CULMEN AND TARSUS

Data on the growth of the culmen and the tarsus were collected from hatchery-reared birds and from wild juveniles and adults. The growth curves of these parts in hatchery juveniles are shown in Figure 6.

The tarsus grew more rapidly than did the culmen, as it does in most birds (Huggins, 1940). A sex difference in the size of tarsus was apparent by two weeks of age. Because the tarsus reached full size when the bird was in its sixth or seventh week of life, it was not a good criterion of age and was measured only in one season.

The culmen reached nearly full size by the tenth week of life. The table below shows that there was no increase in culmen size after 16 weeks of age.

|        | 16 weeks old    | 9 months or older |  |  |  |
|--------|-----------------|-------------------|--|--|--|
| Male   | 47.6 (16 birds) | 47.7 (18 birds)   |  |  |  |
| Female | 45.3 (13 birds) | 45.0 (95 birds)   |  |  |  |

Similar data presented by Hanson (1951a) for the Canada Goose showed that the culmen was no larger in adults than in birds in their first autumn.

Measurements of culmen and tarsus of known-age, dyed, wild juveniles are compared to those of hatchery-reared birds in Table 1 and show close agreement. However, when data secured from wild birds which were marked and recaptured were compared with hatchery data from hatchery-reared birds, the latter seemed to have grown faster than wild birds. This may be a result of small sample size.

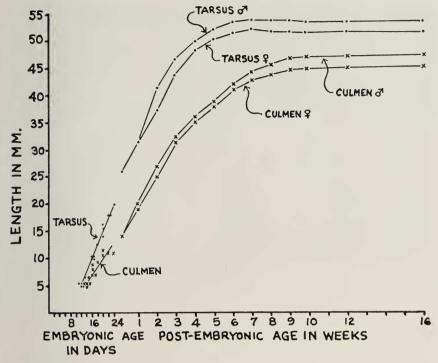


Fig. 6. Cumulative growth in size of culmen and tarsus in juvenal Redheads, and scatter diagram of measurements of embryos.

A comparison of culmen measurements of adult females from Manitoba and Utah showed no significant difference in these populations: 46 females from Utah averaged 44.9 millimeters and 49 from Manitoba averaged 45.1 millimeters. Little geographic variation in size is to be expected because of the mingling and pairing of birds from different areas on wintering grounds, a factor which limits subspeciation in many species of ducks, according to Mayr (1942:241–242).

## DEVELOPMENT OF NATAL AND JUVENAL PLUMAGES

Bent (1923; 1925) was one of the earliest workers to report observations on sequence of feathering in juvenal waterfowl. He included data on Mallard (Anas platyrhynchos), American Widgeon (Anas americana), Cinnamon Teal (Anas cyanoptera) Pintail (Anas acuta), and the Canvasback (Aythya valisineria). Less extensive notes on other species, and comparisons between species, such as the Redhead and Canvasback, also were presented. While his descriptions were incomplete, general patterns were established.

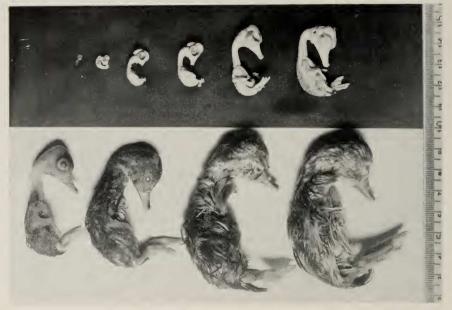


Fig. 7. Redhead embryos ranging from four to 22 days incubation, photographed at two-day intervals.

More detailed information has since been published for the Canvasback (Hochbaum, 1944:103); Wood Duck, Aix sponsa, (Hanson, 1951b); Tufted Duck (Veselovsky, 1951); and Grey Duck, Anas superciliosa, (Cunningham and Welch, 1955). Comparative studies of several species have been made by Heinroth (1928:132–229) and Southwick (1953).

Natal plumage.—Figure 7 shows Redhead embryos at two-day intervals from four to 22 days of incubation. Hatching occurs at 24 to 28 days. according to Hochbaum (1944:90), Peter Ward (pers. comm.), and my own observations.

The rectrices appear at 12 days, followed by the feathers of the spinal and femoral pterylae at 14 days. The capital feathers and remiges are evident at 16 days and the embryo is completely feathered at 20 days of age.

The appearance of the feathers plus other morphological features, such as size, proportion of head to trunk, and development of limbs and bill, serve as excellent criteria for age determination of embryos. These characteristics are apparent in Figure 7.

Upon hatching, the Redhead duckling is the lightest in color of any diving duck (see Kortright, 1943: Plate 34). Considerable variation in color occurs, however; some ducklings are cream and brownish-olive while others are nearly as dark as Canvasbacks. Leg and bill color usually vary with the

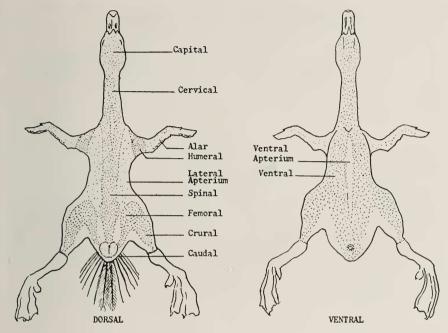


Fig. 8. Pterylography of a downy Redhead.

plumage. Color variation is not widespread, however, and is not due to differences in sexes as reported in the Tufted Duck (Veselovsky, 1951).

Characters for distinguishing Redhead ducklings from those of the Canvasback and Ring-necked Duck (*Aythya collaris*), which they resemble, have been presented by Brooks (1903), Phillips (1925: Plate 59), Todd (1936), Kortright (1943: Plate 34), and Hochbaum (1944:101).

The pterylography of a downy Redhead is shown in Figure 8. In size and position of the apteria of ducklings, the Redhead did not differ noticeably from the Pintail and Mallard.

Color of the natal down gradually fades in the wild. This fading probably varies with weather conditions. Most of the bright color is lost within five to eight days in the wild but remains several weeks in the sheltered, hatchery-reared birds.

Juvenal plumage.—Figure 9 illustrated the sequence of feathering in the juvenal Redhead. These drawings also serve to show the sequence of feathering in the Canvasback, which grows at the same rate as the Redhead (Hochbaum 1944:108). Figure 9 is designed to permit determination of the age of ducklings in the field. The correspondence between the age of the ducklings in weeks and the age classifications commonly used by waterfowl

survey personnel (Southwick, 1953; Gollop and Marshall, 1954) is as follows:

| Age in weeks | Age classification |
|--------------|--------------------|
| 1            | I a                |
| 2            | I b                |
| 3            | I c                |
| 4            | II a               |
| 5            | II b               |
| 6            | II c               |
| 7            | III a              |
| 8            | III b              |

The first feathers of the juvenal plumage are those of the tail, which push out the natal tail feathers at 12 to 14 days after hatching. The natal feathers are continuous with the juvenal feathers and cling to the latter until the teleoptile is partly vaned (Jones, 1907; Beebe and Crandall, 1914; Ewart, 1921), dropping off in wild birds at three to five weeks of age and forming the notched tail feathers useful in determining the age of ducks. The juvenal rectrices are not visible in the field until the birds are nearly four weeks old. Cumulative growth of the tail, as well as the primaries and scapulars, is plotted in Figure 10.

Dyeing ducklings in the eggs was an especially useful technique for rendering conspicuous the changes in down feathering. Juvenal body down develops between the bases of the natal down feathers at two weeks of age. This juvenal down was observed by Veselovsky (1951) in the Tufted Duck. It is not complete in the Tufted Duck until 30 days of age but it completely covers the Redhead by 20 to 25 days. In the Redheard, this down is pale gray on the underparts and medium gray on the upper parts, giving the pattern of the back more contrast than is evident in the natal down.

At two and one-half to three weeks, contour feathers of the auricular region and the flanks and scapulars develop, but these are not usually visible in the wild until the bird is nearly four weeks old. Hatchery birds have a more downy appearance than do wild birds of the same age because down breaks off the juvenal feather earlier in the wild.

At four weeks, the head and back are distinctively marked by the patches of new feathers but most of the upper parts are still downy. The underparts are mostly feathered, only the upper breast and legs remaining downy. The under and upper tail coverts are present, the vanes of the tertiaries are breaking from their sheaths, and the quills of the secondary and primary feathers are breaking through the skin.

By five weeks of age, juveniles of the Redhead are almost completely feathered, with down remaining only on the rump, back, and the base of the neck. The tertiaries and greater, median, and lesser secondary coverts are well developed. The secondaries are present but the vanes are hidden by the overlapping coverts. The primaries are present only as quills.

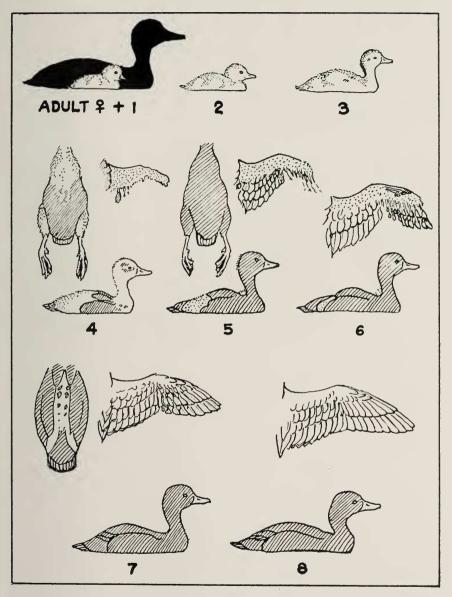


Fig. 9. Sequence of feathering in the Redhead from one to eight weeks old.

At five or six weeks of age, the scapulars and interscapulars of males show delicate white vermiculations or frosting. This is a valuable characteristic for sexing birds and has been used for several years by A. S. Hawkins

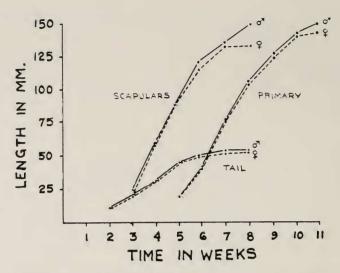


Fig. 10. Cumulative growth of juvenal rectrices, scapulars and primaries.

when banding Redheads. Occasionally females are found with white flecking in this region but only one case was observed which might have been confused with the vermiculations of the male.

Down still remains on the back at six weeks but the rump is well feathered, forming an inverted "V" of feathers pointing toward the head. The primaries are breaking from the tips of the long, bluish quills.

In the seven-week-old Redhead, feathering of the back occurs in two rows from the rump to the interscapular region. The remaining down is covered, however, by the scapulars which now extend beyond their coverts. The white tips of the secondaries are visible when the wing is held loosely in place or flapped but otherwise they are hidden by the scapulars and tertiaries. The sheaths of the primaries and greater primary coverts are still conspicuous.

By eight weeks of age, Redheads are usually completely feathered. A trace of down may remain on the backs of retarded birds. The wing appears complete but the bases of the quills are soft and the feathers not quite fully grown. In advanced birds, as many as half of the primaries may be hardened. Usually the calami of all the secondaries are hard and translucent by this time, as are those of the tertiaries.

Hardening of primaries and the time of flight.—Hochbaum (1944:108) stressed the importance of the age at time of flight to the survival of juvenal waterfowl and presented data for 11 species of hatchery-reared ducks. A summary of published observations of the age at which flight is attained in

TABLE 4 AGE AT WHICH FLICHT IS ATTAINED BY SOME NORTH AMERICAN DUCKS

| Species                          | Age in Days | Authority                          |
|----------------------------------|-------------|------------------------------------|
| DIVING DUCKS                     |             |                                    |
| Redhead                          | 56          | Evans, Hawkins, and Marshall, 1952 |
| Redhead                          | 56-63       | Williams and Nelson, 1943MS        |
| Redhead                          | 56-73       | Present study                      |
| Redhead                          | 63          | Dzubin, 1952                       |
| Redhead                          | 63-70       | Phillips, 1925: 175                |
| Redhead                          | 63-77       | Hochbaum, 1944: 108                |
| Redhead                          | 70-84       | Low, 1945                          |
| Canvasback                       | 54          | Evans, et al., 1952                |
| Canvasback                       | 58-65       | Dzubin, 1952                       |
| Canvasback                       | 63-77       | Hochbaum, 1944: 108                |
| Canvasback                       | 70-84       | Bent, 1923: 194                    |
| Lesser Scaup <sup>1</sup>        | 56-73       | Hochbaum, 1944: 108                |
| White-Winged Scoter <sup>2</sup> | 63-77       | Hochbaum, 1944: 108                |
| Ruddy Duck <sup>3</sup>          | 49          | Stresemann, 1940                   |
| Ruddy Duck                       | 52-66       | Hochbaum, 1944: 108                |
| Goldeneye <sup>4</sup>           | 56          | Stresemann, 1940                   |
| Goldeneye                        | 62          | Millais, 1913                      |
| DABBLING DUCKS                   |             |                                    |
| Mallard                          | 49-60       | Hochbaum, 1944: 108                |
| Mallard                          | 56          | Stresemann, 1940                   |
| Mallard                          | 56-70       | Ewart, 1921                        |
| Gadwall <sup>5</sup>             | 49-63       | Hochbaum, 1944: 108                |
| American Widgeon                 | 45-58       | Hochbaum, 1944: 108                |
| American Widgeon                 | 47          | Evans, et al., 1952                |
| Pintail                          | 38-52       | Hochbaum, 1944: 108                |
| Pintail                          | 49          | Stresemann, 1940                   |
| Pintail                          | 42          | Dzubin, 1952 -                     |
| Blue-winged Teal <sup>6</sup>    | 38-49       | Hochbaum, 1944: 108                |
| Blue-winged Teal                 | 40-47       | Dzubin, 1952                       |
| Blue-winged Teal                 | 42          | Bennett, 1938: 55                  |
| Shoveller <sup>7</sup>           | 39          | Dzubin, 1952MS                     |
| Shoveller                        | 52-60       | Hochbaum, 1944: 108                |

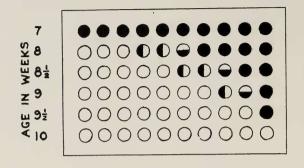
ducks is shown in Table 4. In general, the divers require longer to reach the flying stage than do the dabblers.

Growth and feathering of geese is rapid. Blue and Snow geese (Anser caerulescens) have been reported flying at slightly more than four weeks on Baffin Island by Soper (1930:58) and at five and one-half to six weeks

<sup>&</sup>lt;sup>1</sup>Aythya affinis <sup>2</sup>Melanitta deglandi <sup>3</sup>Oxyura jamaicensis <sup>4</sup>Bucephala clangula

<sup>&</sup>lt;sup>5</sup>Anas strepera <sup>6</sup>Anas discors <sup>7</sup>Anas clypeata

# PRIMARY NUMBER



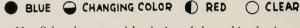


Fig. 11. Color changes and hardening of the rachis of primary flight feathers in juvenal Redheads.

on Southhampton Island by Cooch (1953). The somewhat larger Canada Goose has been recorded as flying at 10 to 11 weeks by Heinroth (1928:178) and seven to eight weeks by Moffitt (1931). Balham (1954MS) observed that nine weeks were required to reach the flying stage but that the time of first flight was influenced by family and flock behavior.

It is difficult to determine the time of first flight of individual birds, either in the hatchery or in the wild. Hochbaum's (1944:103) observations on hatchery birds were based on records of individuals over a period of years but this method was not satisfactory for observing large samples of waterfowl. Also, it is doubtful that the stimulus to fly is as great in an enclosure as it is in the wild, and thus records from captivity may be biased. Therefore, the age at time of flight of large groups of captive birds was estimated by observing the hardening of the shafts of the flight feathers. This occurs as follows: The sheathed feathers ("blood quills") are soft and bluish. The sheath cracks off from the tip to the base and the vane unfolds. When the vane is nearly free, the rachis becomes translucent. The color of the rachis changes from a milky-blue to purple or mottled blue and red and then to pure red. Finally the rachis becomes white and then translucent and hard. The hardening of the remiges follows the sequence of their growth, progressing from proximal to distal remex. A typical pattern is shown in Figure 11.

Field observations showed that flight of wild birds was possible before all primaries had reached the clear stage. Since each proximal remex overlaps each succeeding distal remex, the hardened primaries reinforce each of the soft primaries. In addition, the ratio of body weight to wing area is less in the juvenile than in the adult. Juveniles of 10 to 12 weeks of age with all but two primaries clipped from both wings are capable of short flights. Hatchery-reared birds which were released in the wild flew well with three to five soft primaries and wild-trapped birds with an equal number of soft primaries were able to fly when tossed into the air. This by no means indicates that birds of that age are masters of their wings; several weeks of experience are necessary before the birds are good fliers. However, it may be concluded that Redheads are able to fly when five primaries are clear and hard. The information presented in Table 5 is drawn from observations of hatchery-reared Redheads and shows the age at time of flight as indicated by the presence of five hardened primaries.

TABLE 5

AGE OF HATCHERY REDHEADS AT TIME OF FIRST FLIGHT AS INDICATED BY THE HARDENING
OF THE PRIMARIES

(Data for 1952 and 1953 combined)

| Age                      | Number of Birds |  |
|--------------------------|-----------------|--|
| Eight weeks              | 2               |  |
| Eight and one-half weeks | 29              |  |
| Nine weeks               | 41              |  |
| Nine and one-half weeks  | 13              |  |
| Ten weeks                | 7               |  |
| Ten and one-half weeks   | 1               |  |
|                          | _               |  |
| TOTAL                    | 93              |  |

## POST-JUVENAL MOLTS AND PLUMAGES

Post-juvenal molt and first winter plumage in the male.—Feathers of the first winter plumage make their appearance before the juvenal primaries are fully hardened. Many males have brownish-red feathers in the lores and cheeks at eight weeks of age; these are present in all males at nine weeks. At 12 to 13 weeks conspicuously vermiculated scapular and flank feathers appear (see Color Plate). At 14 weeks, the male's head is more chestnut than buffy brown, about one-fifth of the flank and scapular feathers are of the winter plumage, and a ring of black feathers encircles the neck. New feathers are evident in the breast and belly. At 16 weeks, the breast is conspicuously mottled with black and the head is usually chestnut but varies from pale fuscous to blackish brown in different individuals. The first winter plumage is nearly full by January or February when the birds are six and one-half to eight months old, as was noted also by Bent (1923:80) and Phillips (1925:



Fig. 12. Adult (left) and yearling Redhead males, showing greater amount of white in the breast in the first winter plumage.

64). A few males are still molting upon arrival on the breeding grounds in April and many retain juvenal plumage of the back and venter until their first post-nuptial molt. Dwight (1914) noted spring molt of yearling male Scoters (*Melanitta* spp.) and recognized that it might be delayed post-juvenal molt. Smalley (1915) believed that spring molt in yearling male ducks was merely delayed post-juvenal molt. The entire juvenal plumage of the wing is retained through the first winter but the juvenal tail feathers are shed at three and one-half to seven months and replaced with new, pointed dark gray feathers. No regular sequence of loss is apparent but tail feathers are replaced as they are lost.

The first winter plumage rarely has the brilliance of later winter plumages, as was noted in the Pochard (Aythya ferina) by Millais (1913:15). The light magenta iridescence of the head and the vermiculated feathers of the flank and scapulars are of more subdued coloration than in later years. The juvenal wing is much less frosted with white than is that of the adult, and the white frosting on the greater primary and secondary coverts, median primary coverts, and inner alula feathers is lacking. The line of demarcation between the black breast and white belly is also less clear-cut (Fig. 12).

Post-juvenal molt and first winter plumage in the female.—Color changes in the female are less conspicuous than those in the male because the first winter plumage in females closely resembles that of the juveniles. Plumage changes were observed by parting feathers and clipping them to watch their replacement. Molt and development of the female's first winter plumage is



Fig. 13. Variation in abundance of white feathers on the heads of adult female Redheads.

identical with that of the male.

Distinguishing yearling from adult females is difficult because the adult and juvenal wing feathers are identical. The undertail coverts of yearlings in first winter plumage usually show a pattern of speckled buffy brown on a white background, while those of adults have brownish-olive patches on white. Adults tend to have more frosting of white on the scapulars and usually have white feathers on the back of the head (Fig. 13).

These white head feathers are of particular interest; their numbers seem to increase with age as in hawks (Brooks, 1920), but the most conspicuous change appears to occur during the second fall and winter. Nearly all wild hens have a few white feathers, but captive females rarely do. The location of these feathers suggests that they may develop as a result of damage to the feather follicle when the male pinches the female's head during copulation. However, attempts to induct formation of white feathers in four females by pinching the skin with pliers were unsuccessful.

White head feathers occur less frequently and less abundantly in other members of the genus Aythya in North America and in the European Pochard. Spring molt.—Yearling, as well as older females, undergo a partial molt



Fig. 14. Nest down (left) and winter down feathers of the Redhead.

in late April, May, or early June, just prior to breeding. As a result of this molt, the crown, cheeks, neck, side of the lower neck, flanks, and occasionally scapulars, develop a deep tawny plumage (see Color Plate). Similar feather replacement was noted by Jackson (1915). Smalley (1915), and Schiöler (1921) in several dabbling ducks and by Jackson (1915) and Witherby, et al., (1943:290) in European members of the genus Aythya. Jackson also noted that a special nest down was acquired during the spring molt which was "much longer and coarser than the ordinary down." Measurements of 25 down feathers from six Redhead nests and 25 down feathers from various parts of an adult Redhead female collected in October showed that nest down averaged 22 mm. in length while the autumn down averaged 20.1 mm. Of greater significance was the fact that 100 barbules of nest down averaged twice as long as a like number of barbules of autumn down; it is this difference which causes the more plumose appearance of nest down (Fig. 14). The barbules of down feathers from an immature female in fall were likewise very short. The increased growth of breast down in spring may be a result of higher estrogen levels during the breeding period, a causal relationship demonstrated for the Domestic Chicken (Gallus gallus) by Juhn, Faulkner, and Gustavson (1931). Down feathers acquired in spring are not conspicuously darker than those acquired at other times of the year, as was noted in dabbling ducks and some diving ducks by Jackson (1915) and Bowles (1917).

Plumage of the incubating female.—Six females trapped during incubation



Fig. 15. Variation in color of Redhead nest down feathers (A through D) compared to Canvasback nest down (E) and a nest down feather of a Redhead × Canvasback hybrid (F).

showed no molt or replacement of contour feathers. This was also the case for six Canvasback females captured on the nest. However, some down is continually being replaced. This down has been reported as nearly pure white (Bent, 1925; Hochbaum, 1944; Broley, 1950), but much variation occurs. Individual females had down feathers which varied in color from white to medium gray (Fig. 15). About half of all birds examined had mixtures of white and gray.

Incubation patches have not been reported for members of the Anatidae (Bailey, 1952), but Stresemann (1934:392) wrote that long down develops and is plucked by the female for her nest. This down is probably loosened by physiological changes in the brood patch, such as those demonstrated in sparrows and gulls by Bailey (1952). Preening may then loosen the feathers but I observed no direct plucking by hens. Sufficient down is lost from the abdomen to create an area bare of down (Fig. 16). This condition was apparent in a female captured after nine days of incubation but it probably could be found earlier because most down is added to the nest before incubation begins. In Redheads, the down-free patch may be two to four inches wide and four to five inches long but some Redheads and all



Fig. 16. Incubating Redhead female with ventral feathers parted to show absence of down on abdomen.

Canvasbacks observed were devoid of most down over the entire breast and abdomen.

First-year eclipse and second winter plumage of the male.—The first winter plumage of yearling males becomes dull by late June. In late June or early July, when the bird is about one year old, the post-nuptial molt results in the development of the first eclipse plumage (see Color Plate). Molt and replacement are complete in most birds. The eclipse plumage of the male Redhead more closely resembles its winter plumage than is the case of the eclipse plumage of male dabbling ducks (see Kortright, 1943). Male Redheads become flightless during July and August and renew their body and wing feathers in August and September. The remiges and rectrices are shed and renewed once while the body feathers are molted and renewed twice. I have no evidence indicating that the tail is molted twice as Kortright (1943: 22) states is true of the Mallard. By late September or early October, the males are often in their second winter plumage.

The sequence of molt is as follows: The rectrices are lost irregularly and replaced as they are lost. Thus some feathers are fully grown before others have been shed. Their molt precedes that of the wing and proceeds concurrently with the body molt. The remiges are not lost until the head, neck,

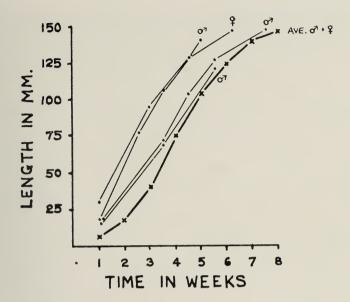


Fig. 17. Growth of the ninth primary in four adult Redheads (fine lines) compared to the average for juveniles (heavy line).

and breast are in nearly full plumage and the flank feathers are being renewed. No definite sequence of molt of the remiges was apparent but all were lost in less than a week. They are renewed in sequence, following the pattern of remige growth in the juvenile—proximal before distal. Remiges of the adult appear to grow at a slightly faster rate than in the juvenile (Fig. 17) and are fully hardened in five to six weeks. The under-wing lining and the axillaries are usually held until the remiges are half grown. The wing coverts are the last to be renewed, the median secondary and central marginal coverts being retained until nearly all other coverts have been replaced. The male wing is then fully adult.

Irregularity of the line of demarcation between black breast and white belly is apparent in the eclipse plumage of yearling birds as it is in the first winter plumage.

Males which desert their females in June in the Delta Marshes fly northward to feeding areas of lakes in northern Manitoba and molt in late July and August. Because some time elapses between the desertion of the female in June and July and inception of the molt and because of the importance of decreasing day-length in regulating molt (Lesher and Kendeigh, 1941), it might be expected that the wing molt would occur at the same time each year. However, there is evidence that the time of molt in the Redhead male is also influenced by seasonal weather patterns and related breeding phe-

nology. This was indicated by the condition of the primaries of adult males shot in Lake Winnipegosis and examined in hunters' bags during 1952, 1953, and 1954. In 1952, 29 per cent of 56 adult males had some soft primaries. The 1953 nesting season was about 10 days later and this was reflected in the molt of the bagged males; 60 per cent of 113 adult males had soft primaries. In addition, the males had much of their eclipse plumage remaining, while most were in nearly full winter plumage in 1952. Nesting was further delayed 10 days in 1954 but the hunting season also was set back 10 days over the previous two years. Nevertheless, an examination of adult males by Game Guardian Sigurdur Oliver of the Manitoba Game and Fisheries Department showed that 68 per cent of 31 males had some soft primaries.

Summer molt of the female.—The female undergoes a single complete molt in late summer that results in the second winter or adult plumage. In Manitoba, females with broods are often in full body molt in August. I have never seen a flightless female with a brood. The nuptial plumage is very faded and worn (see Color Plate) and the new plumage is dark brown. The sequence of the molt occurs as in the male, although perhaps not with the same rapidity. It is usually not complete until October. By dyeing captive birds in midwinter, after the full plumage was acquired, it was found that no main contour feathers were renewed during the winter. Some small feathers, such as those of the head and down feathers, seem to be renewed almost continuously. However, there is no evidence that a double molt occurs in the female in fall as it does in the male.

Adult or second winter plumages.—The adult plumages are shown in the Color Plate and have been described adequately elsewhere. There is little further change once the bird has reached its second winter but the brilliance and distinctness of the winter plumage often improves with age.

The normal cycle of development and sequence of plumages of the Redhead is summarized in Figure 18. The difference between the sexes in the sequence of molt is of special interest. Witherby et al. (1943:290) found similar sequences of molt in the European Pochard and suggested that the plumage acquired by females in spring corresponds with the male's eclipse plumage which is acquired in August. Since this spring plumage is a breeding plumage, it seems more likely that it corresponds to the breeding plumage of the male, which is acquired in September and October following the post-eclipse molt. The non-breeding (=winter) plumage of the female is acquired in late summer and is retained until spring, as in passerines. The non-breeding (=eclipse) plumage of the male is retained only about a month, after which the breeding plumage (which is worn throughout the winter) develops.

The sequence of molting in the male Redhead results in avoidance of molting during migration and in winter and yet the male is in full breeding

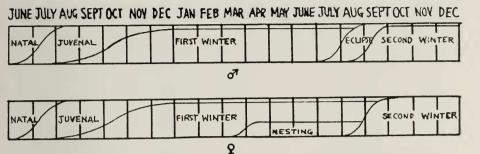


Fig. 18. Sequences of plumages in male (upper) and female Redheads from hatching until the acquisition of the second winter plumage. Height of the curve shows the approximate percentage of the plumage replaced.

plumage when courtship begins on the wintering areas. The evolution and retention of a different sequence in the female is perhaps related to the lesser importance of plumage during courtship and the value of protective coloration and a suitable supply of nest down. Stresemann's (1940) descriptions show that a sequence similar to that of the female Redhead occurs in both sexes of the Ruddy Duck (Oxyura jamaicensis) and in the hen Pintail, but the Pintail drake and Mallards and Goldeneyes (Bucephala clangula) of both sexes molt in a sequence similar to that described above for the Redhead male.

## DEVELOPMENT OF AND SEASONAL CHANGES IN BILL AND EYE COLOR

Sexual differences in eye color are apparent as early as eight to 10 weeks: the iris of the male is a dull straw yellow and that of the female is dull yellow-lime with a brownish center. At 12 to 16 weeks of age, the eye of the male is brighter and that of the female is more brown than greenish. These colors brighten throughout the winter and by April the male's iris is yellow and the female's is sepia.

While wearing eclipse plumage, the male's iris becomes a dull yellow-orange but there is no conspicuous change in that of the female at this season.

No distinct difference in leg color is apparent in members of the genus *Aythya* during the eclipse plumage, such as was found in the Black Duck, *Ancs rubripes*, (Shortt, 1943) and other members of the genus *Anas*. Legs of adults tend to be less greenish and a darker gray than those of juveniles.

Sex differences in bill color also become apparent at eight to 10 weeks. The tip darkens and a vague, transverse white line forms behind the tip. This is more conspicuous in males than in females but not until the following spring does it approach the distinct condition found in the adults. In the male the remainder of the bill gradually lightens and becomes a pale cobalt. During the eclipse period it loses its bluish coloration and becomes blackish

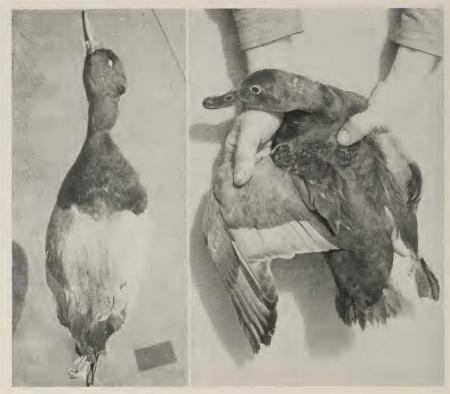


Fig. 19. Male (left) and female Redhead  $\times$  Canvasback hybrids. Note the profile in each and the white feathers of the nape of the female.

gray like that of the female in spring (see Color Plate). The coloration of the male's bill tends to become brighter with age. The female's bill darkens until it is nearly black during late summer.

## PLUMAGES OF SOME HYBRIDS

Cockrum (1952) reported that the Redhead has been known to hybridize in the wild with the Wood Duck, Pintail, and Ring-necked Duck, and McIlhenny (1937) described a bird which apparently was a cross between the Redhead and Canvasback.

Two hybrids were observed in the present study. A wild Redhead male was crossed with a captive Canvasback hen. The offspring were one female and five males but only the female survived beyond the age of one year. Both the male and the female hybrids were intermediate in morphological and plumage characters between the Redhead and Canvasback, resembling

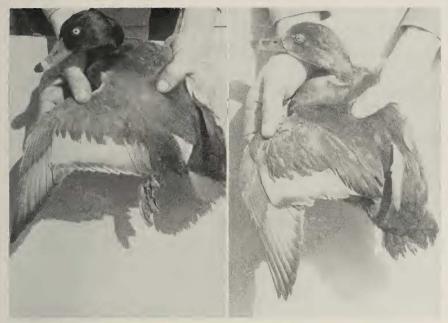


Fig. 20. Male (left) and female Redhead × Ring-necked Duck hybrids. See text for discussion of characters.

the Common Pochard very closely. These hybrids are shown in Figure 19. Of special interest is the white on the head of the female; normally, the Canvasback female has few, if any, white head feathers during adulthood. As is characteristic of the Canvasback, however, the hybrid hen showed much vermiculation on the wing coverts and the scapulars. The first generation hybrid female mated with a Redhead and produced fertile eggs, the young of which resembled downy Redheads. The bills of the second generation hybrids were slightly deformed.

The sexes of the parents of the Redhead-Ring-neck hybrids shown in Figure 20 were unknown. Very apparent in these hybrids were the intermediate body size and voice. The feathers at the base of the culmen were more "V" shaped as in the Redhead rather than "U" shaped as in the Ring-neck (Todd, 1936) and the white ring on the bill was more prominent than in the Redhead. The male's head was brownish black and both the head and the neck had a tinge of chestnut plus a violet iridescence. The back was delicately vermiculated and much darker in color than that of a Redhead. No iridescence was apparent on the secondary coverts of the male as is found in the Ring-neck. The female's plumage contained more gray than is normal for the Redhead, and the lores and eye-ring were whitish as in the Ring-neck. The courtship

behavior of the hybrid male was more like that of the Redhead than the Ringneck—very aggressive and with intensive calling and displaying.

### SUMMARY

This paper describes the growth and sequence of plumages of young Redhead ducks and the weight changes and sequence of molts and plumages in adults. Information was derived from young Redheads reared at the Delta Waterfowl Research Station, Manitoba, wild juveniles which were dyed while in the egg or which were trapped, banded, and later recaptured. For adults, information was obtained from hatchery birds which were kept captive for as long as five years, from wild females trapped on the nest, from birds captured in banding traps, and from others killed by hunters.

Cumulative curves of growth in weight of embryos and juveniles are presented and show typical sigmoid form. However, a decline in weight was noted during the period of remige formation. Males were heavier than females by the second week and remained so throughout life. Hatchery-reared birds tended to be lighter in weight than wild birds of the same age but other development was comparable. Growth of the culmen and tarsus was also recorded and showed a steadier progression than did weights.

Weights of Redheads were influenced by age, sex, and season. In the fall, adult males were heaviest, adult females and immature males were similar in weight, and immature females were lightest. Birds of both sexes lost weight during migration and molt, and females lost during laying and incubation. Minimum weights were reached during the summer molt and maximum weights during the post-molt and pre-migration periods in fall.

Pterylography and sequences in growth of feathers in juveniles are described. A diagram of feather development at weekly intervals, designed to aid in determining age of juveniles in the field, is presented.

Ability to fly was attained at eight and one-half to nine weeks, although the primaries were not fully hardened until the juveniles were 10 to 11 weeks of age. Development of the first winter plumage started before the young were able to fly and was usually complete by mid-winter. A few birds were still molting in early spring after arrival on the breeding grounds.

Sequence of molt was different in the two sexes. The female attained a breeding plumage by a partial molt in spring and a winter plumage by a complete molt in late summer. The adult male, however, had no spring molt but acquired an eclipse (=winter) plumage in late summer and a breeding plumage in fall.

Some features of the plumages of hybrids between Redhead and Canvasback and Redhead and Ring-necked Duck are described.

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